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Piersma, Theunis; Everaarts, Jan M.; Jukema, Joop

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Author(s): Theunis Piersma, Jan M. Everaarts and Joop Jukema

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BUILD-UP OF RED BLOOD CELLS IN REFUELLING BAR-TAILED GODWITS IN RELATION TO INDIVIDUAL MIGRATORY QUALITY[1]

THEUNIS PIERSMA AND JAN M. EVERAARTS
Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands, e-mail: theunis@nioz.nl

JOOP JUKEMA
Haerdawei 44, 8854 AC Oosterbierum, The Netherlands

Abstract. We examined hemoglobin concentration, hematocrit and mean cell hemoglobin concentration (MCHbC) in Bar-tailed Godwits *Limosa lapponica* during the latter half of their staging period in May in the Wadden Sea of The Netherlands. Here they recover from a 4,000–5,000 km long flight from West African wintering areas and refuel in preparation for a flight of similar length toward the arctic Siberian breeding grounds. Hemoglobin concentration and hematocrit levels showed no differences between the sexes, but were higher than expected for a bird species of their size. Bar-tailed Godwits that were on schedule with regard to molt and body mass gains, had elevated concentrations of red blood cells all the time during 19–30 May. In contrast, late-arriving, nutritionally stressed individuals, recognizable by the absence of contour feather molt, showed an increase in both hemoglobin concentration and hematocrit over time before scheduled departure on 1 June, converging to similar values as the group of high migratory quality. There were no time-related and categorical variations in MCHbC. We interpret the relatively low concentrations of red blood cells in late arriving light-weight individuals to indicate that long-distance migration flights may result in light anemia. The quick recovery and maintenance of high hemoglobin and hematocrit levels throughout the latter half of the staging period indicates that high concentrations of red blood cells are as necessary for rapid refuelling as for long-distance flights. The increased viscosity of blood with high hematocrit values was reflected in co-occurring increases in the size of the heart.

Key words: Migration; shorebirds; hemoglobin; hematocrit; body mass; individual quality; heart; Limosa lapponica.

INTRODUCTION

The migration of songbirds and shorebirds over thousands of kilometers of inhospitable habitat between nonbreeding and breeding areas (Moreau 1972, Alerstam 1990), requires the action of a whole array of subtle physiological mechanisms (Ramenofsky 1990, Wingfield et al. 1990, Butler and Woakes 1990, Jenni-Eiermann and Jenni 1991, 1993, Ramenofsky et al. 1995). Some of these are shared with birds facing other environmental challenges, such as living in the cold or living at high altitudes (Dawson et al. 1983). Although long-distance migration, cold stress and the hypoxic conditions of high altitudes might all require adjustments to the oxygen-carrying capacity of blood, this physiological aspect received most attention in comparative studies of circulatory physiology of montane versus lowland birds (Carpenter 1975, Carey and Morton 1976). Only a few authors have explicitly studied changes in blood parameters in relation to migration (Kern et al. 1972, deGraw et al. 1979, Viscor et al. 1985), while several others have hinted at the possibility that migration might affect the characteristics of the blood (Sturkie 1986, Puerto et al. 1990, Prinzinger and Misovic 1994).

The ecophysiological preparations made by long-distance migrants are of two kinds: (1) those related to the accumulation of energy stores, usually fat (Lindström and Piersma 1993), which is necessary to later support the birds during prolonged and uninterrupted flights (Ramenofsky 1990), and (2) those related to the performance of the long-distance flight itself (Butler 1991). During the fuelling phase, the energy stores to carry out the subsequent migratory flight, and in some occasions to survive the lean period following the arrival on breeding grounds afterwards, must be rapidly built up (Alerstam and

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Lindström 1990), a process that may require specific hematological adjustments that allow for the rapid transport of assimilated fuel components toward storage sites. Birds stopping over between two successive long-distance flights may additionally have to do some repair work on tissues that were depleted and damaged during the previous flight (Pennycuick 1978, Goldspink 1991, Evans et al. 1992). Flying is a costly behavior that often takes place at high altitudes with low oxygen pressures (Pennycuick 1989), and we expect the oxygen carrying capacity of the blood to be at its highest at the start of such flights.

Here we examine variation in blood characteristics of a long-distance migrating shorebird based on simple hematological measurements on refuelling individuals of the Bar-tailed Godwit *Limosa lapponica*. The study population winters in tropical West Africa and breeds on tundra in west and central Siberia (Drent and Piersma 1990, Piersma and Jukema 1990). To cover the 8,000–10,000 km separating the tropical wintering and the arctic breeding grounds in spring, most of them make two long flights of about 4,000–5,000 km each, with a stopover for refuelling in the Wadden Sea. Birds not able to make it in only two flights use additional stopovers sites along the route, such as the Atlantic coast of France, and arrive later in the Wadden Sea (Piersma and Jukema 1990). We capitalized on an earlier finding (Piersma and Jukema 1993) that Bar-tailed Godwits refuelling in the Wadden Sea in May come in two types: (1) heavy individuals with fairly complete breeding plumages that undergo an extra molt of contour feathers in the staging area, and (2) lighter individuals with a less complete breeding plumage that show no traces of molt in the second half of May. Members of the latter category may have difficulty in completing the demanding northward migration on time, and a temporal comparison of the blood parameters of the two types might indicate the extent to which blood characteristics change with the nutritional stress imposed by long-distance migration. We concentrated our efforts on the second half of the four-week staging period in May when individuals of high "migratory quality" are recognizable by the presence of molting breast feathers (Piersma and Jukema 1993).

MATERIAL AND METHODS

Bar-tailed Godwits were captured during daytime in the grasslands on Texel, the westernmost Frisian island in the Dutch part of the Wadden Sea (53°03′N, 04°48′E) in May 1995. Birds were captured with a large pull-net, the so-called "wilsternet" (Koopman and Hulscher 1979), developed centuries ago for the capture of Greater Golden Plovers *Pluvialis apricaria*. Bar-tailed Godwits arrive from the West African wintering areas in the last days of April and the first days of May (Piersma et al. 1990), and leave the Wadden Sea in the last days of May and the first of June (average 1 June) for a direct flight to the arctic breeding grounds in Siberia (Piersma and Jukema 1990). Birds were captured on 19 May (the first period, 13 days before departure), 22, 24 and 25 May (the second period, on average eight days before departure) and on 29 and 30 May (the third period, about two days before departure). In the evening of 31 May 1995, a Vee-flight formation of about 20 Bar-tailed Godwits was observed during a highly focal ascent towards the northeast, the direction of Siberia (P. de Goeij, pers. comm.), thus confirming the timing of departure in the year of study.

Within five min after the birds hit the net (mean 3 min, range 2 to 4), blood was sampled from the brachial vein and collected in heparinized micro-hematocrit capillary tubes. The capillaries were immediately stored on ice and analyzed in the laboratory within ten hours. Hematocrit (Ht) was measured after centrifugation at 6,900 × g for 15 min. The average (±SD) total length of the blood measured in two to six capillaries for each individual was 25.9 ± 6.6 cm (range 10.3–41.6 cm). Since only small quantities of blood were available, the hemoglobin concentration [Hb] in the red blood cells was estimated in duplicate on oxygenated hemoglobin using a Lovibond comparator with a cell thickess of 0.1 mm (Harrison 1938). The readings were converted to hemoglobin concentrations (in g/100 ml) using a calibration curve of Lovibond readings plotted on cyanmethemoglobin concentrations (van Kampen and Zijlstra 1961). The Lovibond comparator was calibrated against human, chicken, herring and lugworm hemoglobin. The mean cell hemoglobin concentration (MCHbC) was calculated according to: MCHbC = [Hb]/Ht*100%, where [Hb] is the hemoglobin concentration in g/100 ml and Ht is the hematocrit value in percent cellular fraction of the total blood volume.

After being captured and bled, the godwits were banded and sexed on the basis of plumage and size characteristics (Piersma and Jukema 1990).

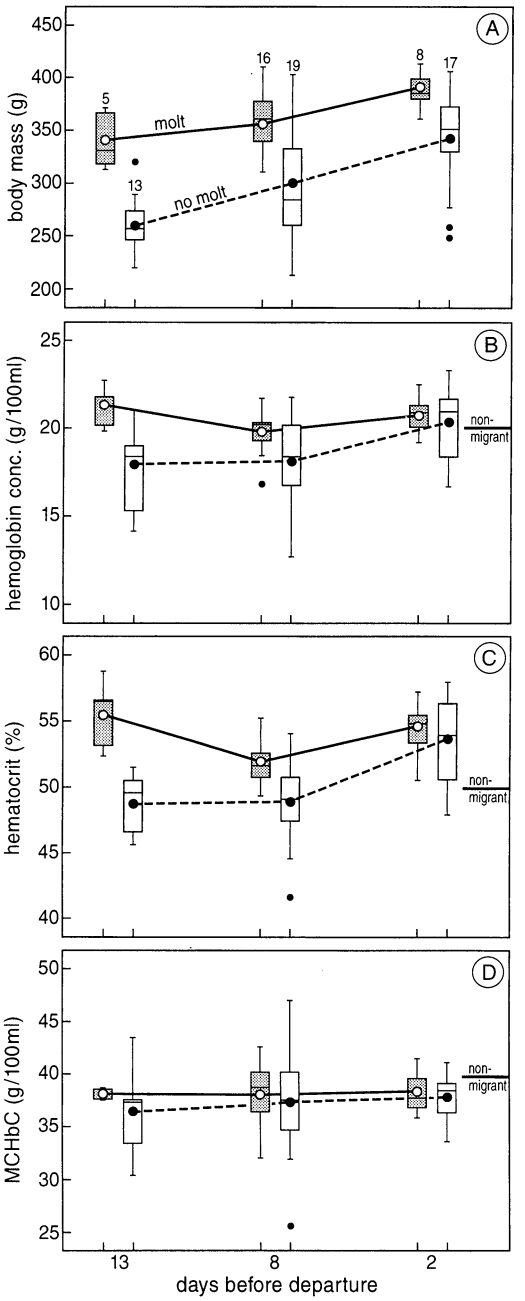

FIGURE 1. Body mass (A), hemoglobin concentration (B), hematocrit (C) and mean cell hemoglobin concentration (MCHbC) (D) in molting and non-molting adult Bar-tailed Godwits staging in the Wadden Sea, The Netherlands, before departure toward the Siberian breeding grounds. Body mass was adjusted for body size differences by dividing individual mass with individual bill length and multiplying it with the average bill length of males (77.9 mm; see text). Shaded boxes indicate birds that showed molt of breast feathers, light boxes indicate birds that showed no molt. Boxes present median values and quartiles, with vertical lines indicating the range and small dots the outliers. Mean values per category are shown by open circles (molting birds) or filled dots (no molt).

The extent of plumage was scored on a scale of one (full winter plumage) to seven (full breeding plumage). The presence of molt on the breast was scored as either absent or present (Piersma and Jukema 1993). In the days before departure, molting birds that had completed contour feather growth were still recognizable by traces of waxy sheaths at the feather bases.

Female Bar-tailed Godwits are 15–20% larger than males (Piersma and Jukema 1990), and to bring the values on body mass together in some of the comparisons we adjusted individual masses for structural size differences to the average male dimension. Over all individuals used in this study the correlation coefficient between bill length and body mass was 0.49. Hence, we used bill length as the linear predictor, by dividing body mass with the individual bill length and multiplying it with the average bill length of the males in the sample (77.9 mm).

A sample of 16 Bar-tailed Godwits (ten males, six females) inadvertedly killed during catches in the period 17–30 May 1989–1992, was compositionally analyzed. Birds were stored frozen and then dissected to organ level. The fresh mass of the heart was taken, and the different parts of the body were dried and their fat extracted using petroleum-ether (boiling at 40–60°C) as the solvent (see Piersma and Jukema 1990 for details of methodology). There was no relationship between fresh mass of hearts ($\bar{x} \pm$ SD = 4.18 ± 0.19 g) and the small amounts of attached fat (0.22 ± 0.09 g). We therefore used fresh mass, adjusted for individual and sex-related differences in structural size as indexed by bill length (see above), or presented as a percentage of total fat-free fresh mass.

RESULTS

The patterns of body mass over time in 1995, and the differences between molting and non-molting Bar-tailed Godwits (Fig. 1A), confirmed the findings of Piersma and Jukema (1993). There was a body mass increase in May in all birds, and non-molting birds remained much lighter than molting individuals. Over all adult individ-

TABLE 1. Results of analyses of covariance of hemoglobin concentration (g/100 ml), hematocrit (%) and mean cell hemoglobin concentration (MCHbC, g/100 ml) in adult Bar-tailed Godwits staging in the Wadden Sea. Time before departure (periods of 13, 8 or 2 days before departure), molt status (presence or absence of breast molt) and sex were entered as factors, and body mass was entered as a covariate.

		Hemoglobin concentration		Hematocrit		MCHbC	
Factor/covariate	df	SS	*P*-value	SS	*P*-value	SS	*P*-value
Time	2	13.8	0.144	90.2	<0.0001	0.2	0.993
Molt	1	12.7	0.059	56.2	0.001	2.3	0.662
Sex	1	3.0	0.355	1.1	0.635	7.2	0.443
Time × Molt	2	12.3	0.178	50.1	0.009	3.2	0.876
Time × Sex	2	4.2	0.548	16.4	0.196	13.6	0.572
Molt × Sex	1	1.4	0.524	4.1	0.364	0.5	0.841
Time × Molt × Sex	2	5.8	0.438	1.7	0.845	16.8	0.502
Body Mass	1	21.7	0.015	67.7	<0.0001	10.1	0.364
Error	65	224.7		318.4		783.9	
R^2		0.43		0.66		0.12	

uals, the mean ±SD hemoglobin concentration was 19.33 ± 2.25 g/100 ml, the mean hematocrit value 51.46 ± 3.48%, and the mean cell hemoglobin concentration (MCHbC) 37.55 ± 3.37 g/100 ml. In the non-molting, but not the molting, birds there appeared to be an increase over time in hemoglobin concentration and hematocrit (Fig. 1B, C). The two indicators of red blood cell abundance seemed to converge to similarly high values in the days before migratory departure. There were no temporal and molt-related changes in MCHbC (Fig. 1D). Two days before departure, the hemoglobin concentration and hematocrit values were somewhat higher than those of a non-migrating, second calendar year bird, with MCHbC being somewhat lower (Fig. 1).

The temporal, molt-, sex- and mass-related differences in the three blood parameters were more comprehensively analysed by analyses of covariance (Table 1). In these analyses, body mass was entered as a covariate after testing for the homogeneity of slopes in a general linear model. There were no significant interactions between body mass and any combination of explanatory variables with hematocrit as the dependent variable. For hemoglobin concentration, the positive effect of body mass was very significant while that of molt was just short of significance. For hematocrit the results were more clearcut, with the effects of time before departure, molt status and body mass all being statistically significant at the 1% level. Of the four interactive terms, only the interaction between time and molt status was significant. This interaction expresses the convergence of the values for molting and non-molting birds before departure (Fig. 1C). For MCHbC, none of the factors or the covariate were significant.

Fig. 2 shows the changes in the relationships between hematocrit and body mass (adjusted to average male size) in the three periods before departure. It stands out that molting individuals are found at the higher body mass (Piersma and Jukema 1993) and hematocrit values. Although the presented slopes relating hematocrit to body mass appeared to decrease with time before departure (Fig. 2), the above mentioned test on the homogeneity of slopes indicated that the differences between slopes were not statistically significant. That, two days before departure, there existed a positive slope at all, depended entirely on the presence of a few non-molting birds with very low body masses in the sample (Fig. 2C). Bar-tailed Godwits that seemed ready to go had hematocrit values of about 54% and a hemoglobin concentration of 20.5 g/100 ml (see also Fig. 1B).

DISCUSSION

The high hematocrit values of Bar-tailed Godwits during a migratory stopover and just before take-off on a long-distance flight confirm earlier reports for waterbirds carrying out similar feats. Banerjee and Banerjee (1977) found no sex differences in hemoglobin concentrations of Ruffs *Philomachus pugnax* wintering in India, but relatively high levels before northward departure. Similarly, Bergmann et al. (1994: pp. 194–195) report high hematocrit values in captive Dark-bellied Brent Geese *Branta b. bernicla* during the

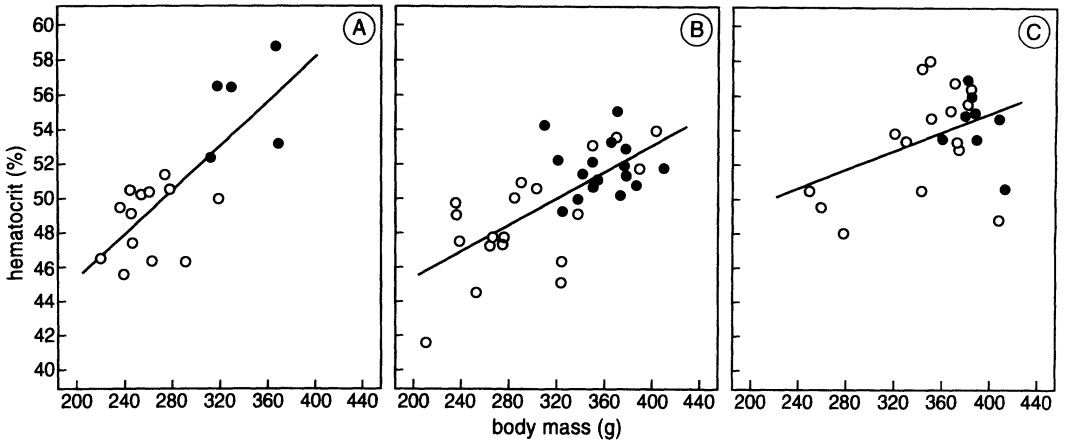

FIGURE 2. Hematocrit (%) as a function of body mass during different phases of the refuelling period of molting (open circles) and non-molting (filled dots) adult Bar-tailed Godwits in the Wadden Sea, The Netherlands. A: 13 days before departure, B: 8 days before departure, and C: 2 days before departure. Body mass was adjusted for body size differences by dividing individual mass with individual bill length and multiplying it with the average bill length of males (77.9 mm). The univariate regression lines given are based on the following equations: A: $Y = 0.064X + 32.5$, $r^2 = 0.58$, B: $Y = 0.039X + 37.6$, $r^2 = 0.49$, and C: $Y = 0.027X + 44.3$, $r^2 = 0.17$. Note, however, that a test on the homogeneity of slopes showed them to be statistically indistinguishable.

migration period during which free-living conspecifics fly in a two-legged migration from the Wadden Sea to arctic Siberia (Ebbinge and Spaans 1995).

In an interspecific comparison of blood parameters in birds, Prinzinger and Misovic (1994) found that body mass was negatively correlated with both hematocrit and hemoglobin concentration. On the basis of their half-logarithmic relationships and a mean body mass of 354 g in our sample of Bar-tailed Godwits, a hemoglobin concentration of 14.8 g/100 ml is predicted rather than the 19.3 g/100 ml that we found. For hematocrit the prediction is 45%, and 51.5% is what we found. With respect to both parameters, migrating Bar-tailed Godwits thus appeared to have concentrations of red blood cells above the average for birds.

That these high hemoglobin concentration and hematocrit values may be interpreted as adjustments for long-distance flights comes from the following findings: (1) the increases in values over time before migratory departure in staging non-molting Bar-tailed Godwits (Fig. 1B, C), (2) the relatively high values in all individuals that are about to leave on a 4,000–5,000 km long flight to the arctic breeding grounds, relative to the value of a non-migrant conspecific (Fig. 1), and (3) the fact that earlier studies have shown that birds requiring high oxygen-binding capacity due to hypoxia and/or flight performance have similarly high values (Carey and Morton 1976, Viscor et al. 1985). The non-molting individuals captured on 19 May with low body masses are likely to have just arrived in the area. We know little about their recent flight history other than that they must have left the West African wintering grounds two to three weeks earlier, and must have covered 4,000–5,000 km in one or more long-distance flights. If Bar-tailed Godwits show a comparable increase in hematocrit before the departure from West Africa, the relatively low values in hematocrit and hemoglobin concentration may thus represent a mild, flight-induced, anemia potentially incurred by all birds during long-distance flights that is rapidly taken care of once the birds have started refuelling (Fig. 1). It appears that building up sufficient levels of red blood cells takes place soon after arrival, well before full body mass recovery. The absence of an additional increase in hematocrit and hemoglobin concentration levels before take-off suggests that high densities of red blood cells are as important during refuelling as they are during long-distance flights at cruise heights with hypoxic conditions.

The interrelationships between hematocrit levels, migration and breeding performance are

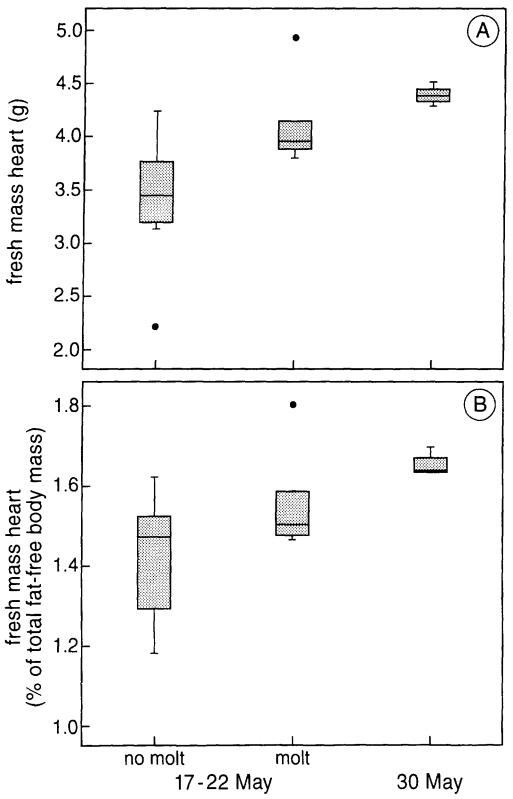

FIGURE 3. Changes in heart size of adult Bar-tailed Godwits staging in May in the Wadden Sea, The Netherlands, with time before departure and with molt status. Birds from 30 May were about to depart for Siberia, and the ones in this sample showed no molt. A: fresh mass of the heart adjusted for structural size differences between individuals by bill length. B: fresh mass of the heart as a percentage of total fat-free mass. Boxes present median values and quartiles, with vertical lines indicating the range and small dots the outliers. *n* values are respectively 7, 6 and 3.

less clear. Two subspecies of White-crowned Sparrows *Zonotrichia leucophrys* showed particularly high hematocrit values prior to and just after their migration to the breeding grounds, with levels being less elevated during post-breeding migration (Wingfield and Farner 1980, Morton 1994). Since Bar-tailed Godwits have to make similarly impressive flights during southward as during northward migration, a comparison between godwits staging in the Wadden Sea in spring and in fall, when they are more difficult to catch, could indicate the generality of particularly elevated hematocrit values during a migration into the breeding areas. If the sparrow pattern were confirmed, it would suggest that a migration towards the breeding grounds comprises a more difficult physiological performance than the return migration.

The high hematocrit level of molting Bar-tailed Godwits and those that are ready to depart enhances the oxygen-carrying capacity of the blood but also makes it more viscous (Vogel 1992). This means that additional cardiovascular adjustments are necessary for the blood to be pumped: blood with a high viscosity requires larger, more powerful hearts (Vogel 1992). This explains why montane birds have higher hematocrit as well as larger relative heart sizes than lowland birds (Carey and Morton 1976).

A sample of 16 staging Bar-tailed Godwits from the Wadden Sea in the second half of May allows us to examine whether heart size and hematocrit levels are also correlated in these migrants. More to the point is the question of whether molting birds and birds just before departure (i.e., the categories that show high hematocrit levels) carry larger hearts than non-molting birds with blood of lower viscosity. Despite the small sample sizes, the hearts of birds ready to depart were indeed larger than hearts of molting birds halfway through the staging period, which were larger than hearts of non-molting birds (Fig. 3). The differences between the three categories were (just) statistically significant, both when heart size was adjusted for structural size differences between individuals (Fig. 3A; ANOVA, $F_{2,13} = 4.877$, $P = 0.026$) and with heart size relative to total fat-free body mass (Fig. 3B; ANOVA, $F_{2,13} = 3.667$, $P = 0.055$). The build-up of red blood cells during refuelling thus seems to be accompanied by a build-up of heart muscle allowing the increasingly "thick" blood to be pumped around at adequate rates.

For reasons of timing and nutrition, some Bar-tailed Godwits staging in the Wadden Sea do not implement a second molt of breeding contour feathers (Piersma and Jukema 1993). The results presented here indicate that they suffer more physical shortcomings than a low body mass and an incomplete plumage alone. Two weeks before departure, their red blood cell levels are still below that of individuals "on schedule." If the substandard quality of their blood and their relatively small hearts inhibit compensatory rates of body mass gain, such birds may be trapped in a negative nutritional and physiological spiral that fails to show up in Fig. 1A because cohorts of

molting and non-molting birds on successive dates are not closed. The proper timing of cardiovascular adjustments is an important physiological challenge for long-distance migrant birds.

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